EVAPORATION AND PLANT SUCCESSION[1]

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 147

GEORGE DAMON FULLER

(WITH SIX FIGURES)

The plant associations on the sand dunes of Lake Michigan have been described by COWLES (1), who has called attention to the succession which is here so strongly marked and so easily determined. In much of the region immediately south of the lake, the forest succession consists principally of associations dominated respectively by cottonwood, pine, black oak, white and red oak, and beech in the order named. These are usually designated the cottonwood, pine, and oak dunes, and the oak-hickory and beech-maple forests. They represent the major associations in a succession extending from the pioneer trees to the climax mesophytic forest formation of the region. The dynamic physiography and the details of the composition of the various stages in the succession have been so thoroughly discussed by COWLES that little further elucidation is necessary, but hitherto no attempt has been made to obtain any quantitative determination of any of the factors influencing this succession.

The researches of LIVINGSTON (2) and others have shown that the evaporating power of the air is a rather satisfactory summation of the atmospheric factors which determine the growth of plants during that portion of the season free from frost, and that it can be accurately measured by the porous-cup atmometer; accordingly, in the spring of 1910, a number of observation stations were established upon the sand dunes near Millers, Ind., and the rate of evaporation was determined during the ensuing growing season. Both the porous-cup atmometer devised by LIVINGSTON (3) and the type described by TRANSEAU (4) were employed in this investigation. They were mounted in wide-mouthed bottles having a

[1] A preliminary report of evaporation studies in the plant associations upon the sand dunes of Lake Michigan.

capacity of 500 cc., closed with tightly fitting cork stoppers that were perforated for the atmometer tubes and for bent capillary glass tubes which served to equalize the atmospheric pressure within the bottles with that of the exterior air, without causing any loss by evaporation or permitting rain water to enter the reservoir. The bottles were sunk in the soil about two-thirds of their height, so that the evaporating surface of the instruments was 20–25 cm. above the surface of the soil. Except where otherwise specified, the readings were made weekly by filling the bottles from a graduated burette to a file scratch on the neck. The small area of the water surface at this point made the probable error in readings less than ± 0.5 cc., and this could have had no appreciable effect upon the results. The instruments were all standardized to the same unit before being used, restandardized at intervals of 6–8 weeks during the season, and a final correction made on their being collected in the autumn. By the coefficients thus obtained all readings were reduced to the standard adopted by LIVINGSTON (**5**) in his recent paper on the operation of the porous-cup atmometer. The directions given in that article were so closely followed that it is unnecessary to detail further the methods used in operating the instruments. Two or three atmometers were discarded during the season on account of various irregularities in their operation, but others either maintained a uniform rate of water-loss or showed a variation that progressed uniformly at a readily calculable rate. To provide still further against the possibility of serious error, two instruments were often maintained a few feet apart at the same station, and several stations were usually established in the same association, the mean of the various readings being taken as giving the true measure of the evaporating power of the air for that association.

No correction has been made for errors caused by rainfall, although during showers some water undoubtedly passes through the porous cup and into the reservoir, because it was thought that the amount of variation thus produced would be the same for all stations within so limited an area, and hence the comparative relation of results would remain unchanged. This assumption has been largely verified by BROWN (**6**), using an atmometer with a rain-

correcting valve. It is the intention of the writer, however, to employ this improved atmometer, also devised by LIVINGSTON (**7**), in the continuation of these studies.

Fifteen different stations were established in the various associations, care being taken to select spots which possessed the average amount of tree, shrub, and herbaceous vegetation characteristic of that specific association as a whole. Owing to a variety of accidents and other circumstances, all the stations did not give equally satisfactory and continuous records; hence the present preliminary report is confined almost entirely to the results from 10 stations in 4 different associations. Many of these records extend from May 6 to October 31, or over a period of 178 days; at other stations the record begins at a somewhat later date, but continues until the severe frosts of November 1, and includes the important part of the growing season for all except a few very early spring plants.

In order to facilitate comparisons between the various stations, and to exhibit the progress of the evaporation rate during the entire season, the average water-loss per day between the weekly readings has been calculated, and the results expressed in graphs with ordinates representing the number of cubic centimeters lost per day by a standard atmometer, the abscissae being the intervals between the weekly readings. The readings included within each calendar month are indicated at the top of the diagram. For convenience of reference, the stations are numbered consecutively, beginning with that nearest the lake shore.

The first group of stations was upon some slowly moving dunes directly north of the village of Millers, Ind., and between the southern shore of Lake Michigan and the Grand Calumet River. According to old maps, this river formerly discharged its waters into Lake Michigan very near the spot selected for one of these stations. Any such discharge has long since ceased, and its exact location has been entirely obscured by the advancing dunes, leaving the remaining river bed as a shallow channel in which the water has little or no current, the present discharge being some eight miles farther west. Dunes are now advancing into this channel at several points, and within a few years will doubtless occupy other portions

of its bed. Here, at a distance of 100 to 200 meters from the shore, the pioneer tree association becomes established, and persists upon dunes of variable size that are usually more or less actively moving. This association is characterized by a paucity of species, all having strongly xerophytic structures. *Populus deltoides*, *Salix glaucophylla*, *S. syrticola*, *Prunus pumila*, and the two grasses *Calamovilfa longifolia* and *Ammophila arenaria* are at this point the only conspicuous members of this rather open cottonwood dune association. In it, upon dunes that have become almost completely fixed, two stations were established on May 6, and a third on July 9, and at the three stations at least four instruments were maintained in constant operation until the last day of October. These stations were about 200 meters from the lake shore, some 100 meters apart, and about 12 meters above the level of the waters of Lake Michigan. At all stations the atmometers received a small amount of shade for a few hours of the day, and on account of the open nature of the association were little sheltered from the wind, the cups receiving a rather sharp sand blast during high winds. Station no. 1 had some sheltering groups of cottonwoods on a slight elevation of sand a few meters southeast of the instruments, and no. 3 possessed a similar but smaller shelter at the southwest. These differences of exposure to winds probably caused some of the variations in the records of the different stations, but affected very slightly the average rate for the season.

The graphs for three cottonwood dune stations have been plotted upon the same chart (fig. 1), and exhibit a great similarity in their general course and in their simultaneous maxima and minima. The rainfall at Chicago (20 miles distant) for the same period, expressed in centimeters, is shown for periods corresponding with those of the intervals between the evaporation readings, but as there seems to be no very exact correspondence between the amount of precipitation and the amount of evaporation, these data are omitted from the other charts. There is certainly a correspondence between the number of hours of cloudy or rainy weather and the amount of evaporation, but this has not been exactly determined, nor does it seem important in our present studies. The evaporation graphs indicate that the most critical period occurs

about the end of July, and this is also toward the end of a period of seven weeks with very little rainfall; hence it may be safe to assume, even without any direct data regarding soil-moisture, that

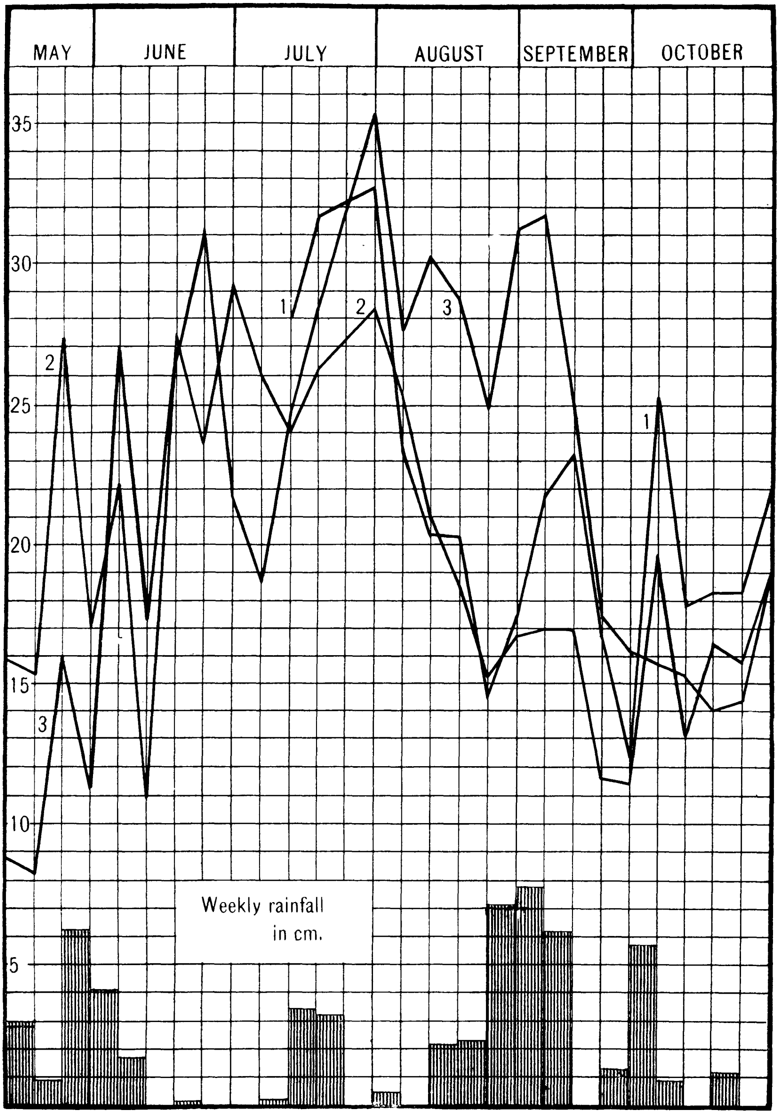

FIG. 1.—Evaporation rates in the cottonwood dune association at stations nos. 1, 2, and 3.

at this time there is a maximum demand by the atmosphere upon the water contained in the plant tissues, while at the same time only a minimum supply is available to replace such losses by transpiration. Two other periods of high evaporation are found to occur, one late in June and the other early in September. The latter is doubtless the one of greater stress, for it follows a month of very low rainfall. It will be seen that the maximum average evaporation for any week is just above 35 cc. per day, and that the minimum only once falls below 10 cc. per day. The average rate for the three stations upon the cottonwood dune for the 178 days of observation is 21.1 cc. per day.

The graphs (fig. 1) indicate that not only is the cottonwood dune an association with a very high rate of evaporation, but also that it is subject to excessive variation. This is most noticeable during May and June, but to a less marked extent prevails through the season, the fluctuations being decidedly greater than in the other associations (fig. 4). The mean of the readings of these three stations is believed to express most accurately the true measure of the evaporating power of the air during the growing season in the cottonwood dune association, and is therefore plotted and used in comparison with similar graphs from the other associations (fig. 4).

As the dunes gradually become fixed, an association dominated by evergreens succeeds the cottonwood dune. This pine dune association varies somewhat in composition in different localities, but in the area under consideration is dominated by *Pinus Banksiana*, associated with *Juniperus virginiana*, *J. communis*, and in the older portions containing also *Pinus Strobus*. In the undergrowth *Arctostaphylos Uva-ursi* is conspicuous, associated with *Rhus canadensis*, *R. toxicodendron*, *Prunus virginiana*, *Celastrus scandens*, seedlings of *Quercus velutina*, *Smilacina stellata*, *Asclepias tuberosa*, *Monarda punctata*, and other woody and herbaceous plants. Two stations were placed in this association at spots of medium density of growth about 100 meters south and east of the cottonwood dune series, but owing to several accidents only one record is worth reporting. This, from station no. 4, is unbroken for 178 days, and is often the mean of the readings from two atmometers.

This association is unique in the dominance of conifers, but is also notable for the comparative abundance of its undergrowth, although many species have decidedly xerophytic characters. That it is a comparatively short-lived association is evident from the presence of seedlings of *Quercus velutina*, the dominant tree of the succeeding association, very early in its history. Comparing the graph of its evaporation with that of the cottonwood dune (fig. 4), it will be seen that it is much lower, never reaching 20 cc. per day, and is subject to less violent fluctuations. Its maxima and minima are nearly synchronous with those of the cottonwood dune. The maximum evaporation rate is 17.5 cc. per day, the minumum falls below 4 cc., and the average for the season of 178 days is 11.3 cc. daily.

Proceeding inland from the lake shore, the pines gradually decrease in numbers, and the black oak, *Quercus velutina*, becomes more plentiful, until at a distance of about 500 meters south of the last station it forms an almost pure stand with only occasional trees of white oak, *Quercus alba*. The shrubby undergrowth consists principally of *Prunus virginiana*, *Rosa blanda*, *Viburnum acerifolium*, *Vaccinium pennsylvanicum*, *Ceanothus americanus*, and seedlings of *Quercus velutina* and *Q. alba*. Among the herbaceous members of the association are *Smilacina stellata*, *Lupinus perennis*, *Tephrosia virginiana*, *Lithospermum canescens*, *Asclepias tuberosa*, *Helianthemum canadense*, *Polygonella articulata*, and *Aster linariifolius*. In this oak dune association four stations were placed within a range of 100 meters; no. 6, on a fixed dune 15 meters high, well covered with the oak forest; no. 7, on a slope at an altitude of about 8 meters; and nos. 8 and 9, on the general floor of the forest some 5 meters above the level of the lake waters. All were about equally exposed and shaded. No. 6 was established on May 6, and the other stations on May 26. Station no. 9 was subject to so many interruptions that no report of its evaporation is presented, but the graphs from the other three (fig. 2) show a very close agreement, with differences corresponding directly to their elevation. A maximum of nearly 19 cc. per day occurred in May during the second week of the record, before the trees were in full foliage. The absence of leaves would largely account for this excessive rate,

but as it occurred when only one instrument was recording, it may be regarded as lacking confirmation, and as it could hardly be a critical period on account of the abundant water supply in the soil, it is disregarded in the general discussion. Throughout the remainder of the season the rate is rather high, but not subject to great fluctuations. A minimum of about 5 cc. per day is reached in September, and is followed by a distinct rise as defoliation pro-

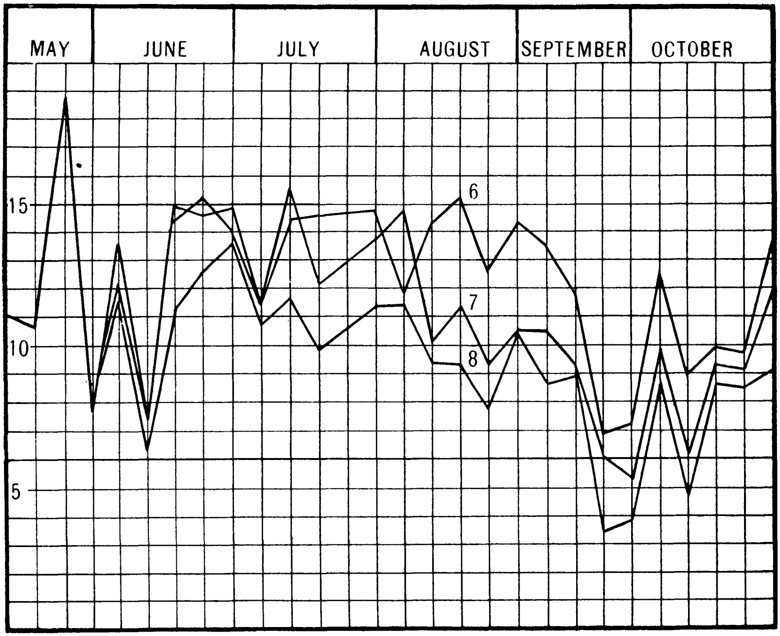

FIG. 2.—Evaporation rates in the oak dune association at stations nos. 6, 7, and 8.

gresses. Station no. 9 (not plotted) gives a somewhat higher rate during July, affording a maximum for that month and for the summer of 16 cc. per day. The average rate for the whole period is 10.3 cc. per day. The mean of all stations in the oak dunes is used (fig. 4) in comparison with similar graphs from the other associations.

At Millers, Ind., the vegetation exhibits no undisturbed successional stages beyond the oak dune, but 15 miles farther east, near the village of Otis, Ind., there is a tract of the climax deciduous

mesophytic forest dominated by the beech, *Fagus grandifolia*, and the maple, *Acer saccharum*. These two species form at least 85 per cent of the tree growth, with the remaining 15 per cent composed of *Tilia americana*, *Ostrya virginiana*, and *Prunus serotina*, and occasional trees of *Quercus rubra*, *Platanus occidentalis*, and *Liriodendron Tulipifera*. The undergrowth is largely seedlings of the dominant tree members of the association, together with *Cornus alternifolia*, *Viburnum pubescens*, *Asimina triloba*, *Sambucus racemosa*, and such herbaceous forms as *Trillium grandiflorum*, *Dicentra*

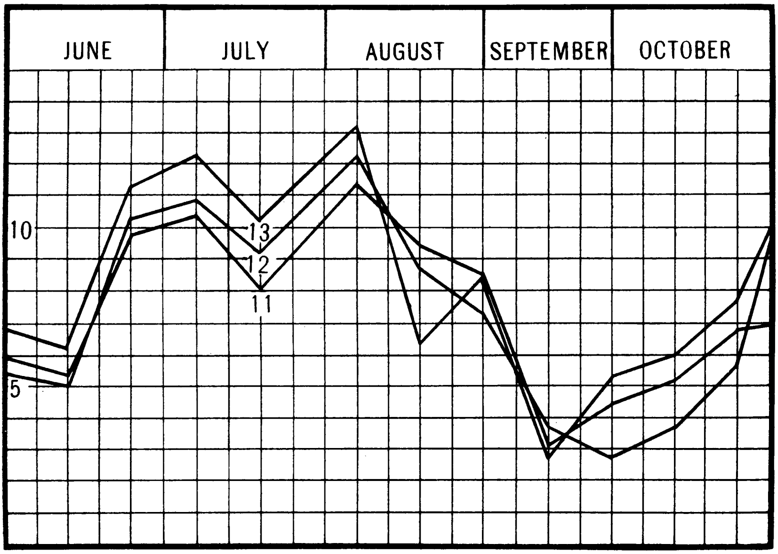

FIG. 3.—Evaporation rates in the beech-maple forest association at stations nos. 11, 12, and 13.

canadensis, *Adiantum pedatum*, *Asplenium angustifolium*, *Polystichum acrostichoides*, *Viola rostrata*, *Impatiens biflora*, *Erigenia bulbosa*, and *Epifagus virginiana*. As this represents the climax formation for a large portion of the United States, it was regarded as a standard to which other plant associations could be referred, and accordingly 3 stations were established in it on May 30, and maintained until the end of October, giving a continuous record for 155 days. On account of the difficulty in reaching these stations, readings were made only every second week throughout

the season. Of the 3 stations in the beech-maple forest, no. 11 was in an area dominated by the sugar maple and well surrounded by maple seedlings. No. 11 was near a large beech tree on a slope covered with *Asplenium angustifolium* and *Impatiens biflora*, while no. 13 was in the midst of beech seedlings between two large trees of the same species. Together they seemed to represent the average conditions in a beech-maple forest. The resulting graphs (fig. 3) are very similar, showing coincident maxima and minima differing but little in amount. The maxima are in July and August, and amount to little more than 12 cc. daily; the minimum occurs in September and is scarcely 3 cc. per day. The average rate of evaporation at the 3 stations for the 155 days is 8.1 cc. per day.

It is here interesting to note the close correspondence between the records for this beech-maple forest and those obtained by TRANSEAU (**8**) in a mesophytic forest containing a small percentage of beech and situated on Long Island, N.Y., where for the period of observation from June 5 to July 2, 1907, the evaporation rate averaged 8.5 cm. daily, compared with 8.4 cm. daily during the month of June, 1910, in the Otis, Ind., forest. While it is not safe to draw any very definite conclusions from records covering but a single month, it may be assumed that the two associations differ very little in the amount of mesophytism developed.

Several methods may be employed in comparing the data obtained from the various evaporation stations. Perhaps the best is to plot upon the same chart graphs representing the mean daily evaporation by weeks, from the several stations in the different associations (fig. 4). It will be seen that the graphs show several similarities, but more differences. The maxima and minima are generally coincident in time and proportionate in amount. All show great irregularity during spring and autumn, and a comparatively high rate during July and August. The general height of the different graphs probably gives the most instructive and interesting differences in the various habitats. That of the cottonwood dune is farthest removed from those of the other associations, and shows a habitat not only with great evaporating power, but one of great extremes, the difference in rate between

two consecutive weeks being nearly or quite 10 cc. per day during May and the first part of June, and on two occasions amounting to an increase of 100 per cent in one week as compared with the preceding. This occurring early during the growing period would doubtless be very unfavorable for the development of any seedlings, especially as it was followed by the very high rates of the succeed-

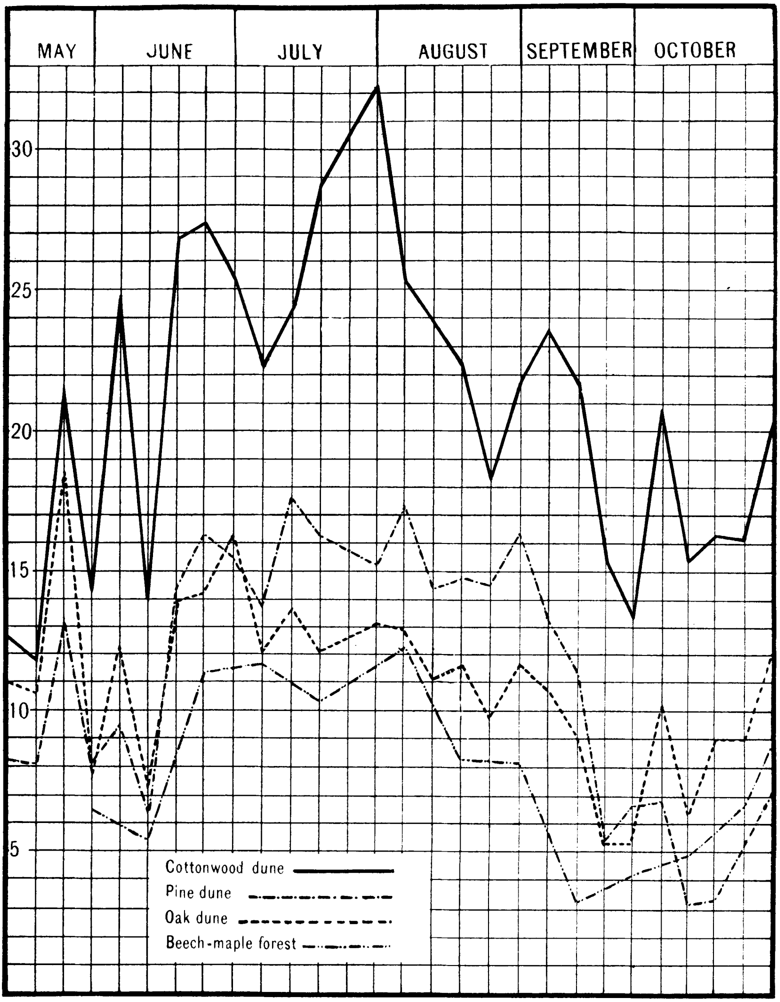

FIG. 4.—Mean daily evaporation rates in the sand dune plant associations and in the beech-maple forest.

ing months. The high maximum occurring at midsummer would probably prove the excluding factor for all mesophytic plants, even if not combined with such other factors as the deficiency of soil water at the same time. Such a graph seems to depict rather well a habitat of atmospheric extremes making large demands upon all available water, and naturally and necessarily resulting in a xerophytic plant association, with a very limited undergrowth and an almost entire absence of herbaceous plants and seedlings. Perhaps nowhere could an association be found so entirely dependent upon vegetative reproduction for its maintenance, for almost without exception any increase in vegetation is the result of subterranean branches.

The graph for the pine dunes is decidedly lower and more regular in its contour than that of the association which it succeeds. Its four nearly equal maxima would indicate that within its limits there was throughout the summer season a continuous stress rather than a series of violent extremes. On the whole, it shows a water-demand of little more than half of that occurring in the cottonwood dune. Its greatest divergence is plainly due to the evergreen character of its vegetation, and is seen in its low range in May and the first part of June, and again in October, when it falls below that of the oak dunes and is even less than that of the beech-maple forest. This would give good reasons for expecting to find within this association truly mesophytic plants, whose activities are limited to the early spring.

The graph from the oak dune stations shows two surprisingly high points; one during May, that may be partially explained by the absence of foliage; and the other near the end of June, which seems to coincide with maxima in the other associations. On the whole, it is more moderate during the months of summer than that of the pine dune, but the difference is not so great as to make it surprising that its undergrowth differs but little from that found in the pine dune association.

The graph from the beech-maple forest stations is one of moderate height and great regularity. It is but fair to say that weekly readings would probably have introduced some minor irregularities, but without changing its general course or influencing the

average rate for the season. At no point does it reach to half the height of that from the cottonwood dune, but surpasses that of the pine dune in October.

The data of these observations relate only to the stratum of vegetation immediately above the surface of the soil, and would be quite different at a height of one or two meters. This lower stratum, however, is the critical one for a forest association, for the development of tree seedlings occurs within its limits, and

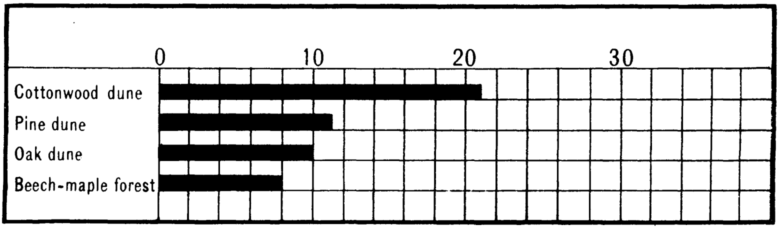

FIG. 5.—Diagram showing the comparative evaporation rates in different associations on the basis of the average daily amount from May 6 to October 31, 1910.

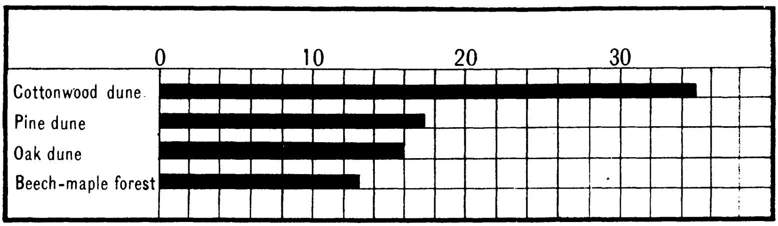

FIG. 6.—Diagram showing the comparative evaporation rates in different plant associations on the basis of the maximum average amount per day for any week between May 6 and October 31, 1910.

therefore it is the portion of the habitat which determines the forest succession and hence the most important ecologically. A single example may be cited from the meager data obtained during the past season regarding the rates of evaporation in the more elevated strata. Very near station no. 13 in the beech-maple forest, an instrument was established 2.5 meters above the surface of the soil, and showed for the season an average of 12.7 cc. daily, as compared with 9.1 cc. daily for no. 13, whose atmometer was 20 cm. above the surface.

The comparative rates of evaporation in the different plant associations may be compared in other ways. If the average amount of water lost by the standard atmometer daily throughout the season be taken as a basis and represented in a diagram giving the loss in cubic centimeters (fig. 5), a graphic representation results which, however, tells little more than what has been shown differently in fig. 4. Likewise, the maximum daily rates for the week of greatest evaporation during the season gives a similar representation of the conditions in the several plant associations (fig. 6). Upon a percentage basis, with the average rate per day throughout the season in the beech-maple forest taken as a unit, the comparative evaporation rate in the oak dune is 127 per cent, in the pine dune 140 per cent, and in the cottonwood dune 260 per cent. As the months of July and August probably represent the critical portion of the growing season with reference to its water supplies, a comparison like the preceding might be made for those months only, when it would be found that the comparative evaporation in the oak dune would be 113 per cent, in the pine dune 146 per cent, and in the cottonwood dune 230 per cent.

Summary

1. These data represent the evaporation rates in the lower but critical stratum of the plant associations.

2. Evaporation at different stations in the same plant association exhibits variations similar in character and degree.

3. The rate of evaporation in the cottonwood dune association, both by its great amount and by its excessive variations, seems a sufficient cause for the xerophytic character of the vegetation and for the absence of undergrowth.

4. Evaporation in the pine dune association exceeds that in the oak and beech associations except when the latter are devoid of foliage.

5. The vernal vegetation of the pine dune is quite as mesophytic as that of the succeeding association, thus agreeing with its lower evaporation rate during that portion of the year.

6. Evaporation in the various associations varies directly with the order of their occurrence in the succession.

7. The differences in the rates of evaporation in the various plant associations studied are sufficient to indicate that the atmospheric conditions are efficient factors in causing succession.

Conclusions

From the study of the data available, it seems evident that the porous-cup atmometer measures with very considerable accuracy the atmospheric factors which combine in making demands upon the water-supply of the aerial portion of the plant; the data, therefore, may be directly related to the plants in an association, and used in determining the comparative xerophytism of plant habitats in so far as they are determined by atmospheric conditions. In such determinations it would appear that the true measure of the limiting atmospheric factors must be found either in the demand throughout the entire growing season as expressed in the average evaporation rate for that period, or in a maximum demand of several days' duration occurring at a period when the water-supply in the soil is deficient, such as would be expressed in a high rate continuing for a week or more in the latter part of the summer. In the associations studied, these demands show practically the same ratio when compared with one another (figs. 5 and 6). If this be the case, we have in the Livingston or Transeau atmometers instruments of sufficient precision to furnish the most valuable quantitative data in the study of plant associations.

A complete study of the water relations of a habitat may be obtained by combining the data supplied by the atmometer with quantitative determinations of the available soil-moisture. It is hoped that some such data may be available in the near future.

It seems highly desirable, in investigations of this character, that the different investigators employ instruments standardized to the common unit recommended by LIVINGSTON (5), and further that a plant association of wide distribution be used as a basis of comparison, and that the conditions in other associations be expressed in terms of these units whenever it is possible to do so. As no association is more widely spread in the United States than the climax mesophytic forest which is frequently characterized by the presence of either *Acer saccharum* or *Fagus grandifolia*, or

both, so no unit seems so well suited for this purpose as the beech-maple forest association or its ecological equivalent. Thus it may be said that the atmospheric conditions in the lower stratum of the cottonwood dune association during the growing season are 260 per cent as severe for plant life as those in the same stratum of the standard association (the beech-maple forest) during the same period.

The writer hopes to continue and extend these investigations during the coming seasons.

Grateful acknowledgment is made of the helpful advice and suggestions of Dr. HENRY C. COWLES, under whose direction this investigation has been conducted.

THE UNIVERSITY OF CHICAGO

LITERATURE CITED

1. COWLES, H. C., The ecological relations of the vegetation of the sand dunes of Lake Michigan. BOT. GAZ. **27**:95–117, 169–202, 281–308, 361–391. 1899.
2. LIVINGSTON, B. E., Evaporation and plant habitats. Plant World **11**:1–10. 1908.
3. ———, The relation of desert plants to soil-moisture and to evaporation. Carnegie Institution of Washington, Publication no. 50. 1906.
4. TRANSEAU, E. N., A simple vaporimeter. BOT. GAZ. **49**:459–460. 1910.
5. LIVINGSTON, B. E., Operation of the porous-cup atmometer. Plant World **13**:111–119. 1910.
6. BROWN, WM. H., Evaporation and plant habitats in Jamaica. Plant World **13**:268–272. 1910.
7. LIVINGSTON, B. E., A rain-correcting atmometer for ecological instrumentation. Plant World **13**:79–82. 1910.
8. TRANSEAU, E. N., The relation of plant societies to evaporation. BOT. GAZ. **45**:217–231. 1908.